SILURIAN GIRVANELLA FROM THE WELSH BORDERLAND

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ABSTRACT. A general survey of the calcareous algae from Silurian limestones of the Welsh Border has yielded many algal remains particularly of the genus *Girvanella*. Nine species of this genus are here described, eight of which are new; and they are grouped according to their size and mode of growth. The Sarmenta group includes three new species, *G. sarmenta*, *G. fragila*, and *G. prolixa*; the Problematica group two new species, *G. pusilla*, *G. incompta* as well as *G. problematica* and its var. *lumbricalis*; the Media group with one new species *G. redia*, and the Ramosa group two new species *G. ramosa* and *G. effusa*. The basis for subdividing the genus is given and the distribution of the specific forms in the varied lithology of the limestones are recorded.

A GENERAL survey of the calcareous algae present in the Silurian limestones of the Welsh Border has shown that algae are more abundant and widespread than has hitherto been recorded. Specimens were collected from numerous localities within the area demarked approximately by Wenlock Edge to May Hill and Dudley to Old Radnor (text-fig. 1).

Previous records of algae in this area are few and the belief that algae contributed to the formation of reef limestones was largely unproved. From the Woolhope Limestone, Garwood and Goodyear (1918) described algal limestones at Old Radnor and Nash Scar; also Garwood (1931) mentioned an undescribed *Solenopora* at Woolhope. *Girvanella* is not recorded by Squirrel and Tucker (1960) in an account of the geology of the Woolhope Inlier.

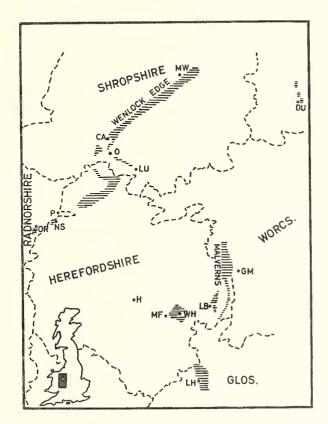
For the Wenlock Limestone, Wethered (1890, 1893) described algae at May Hill, Ledbury, and Purley (West Malverns). Chapman (1907) and Crosfield and Johnston (1914) recorded algae or algal fragments at Dudley. Several authors have indicated the presence of algal limestones as opposed to brachiopod, crinoid, or other facies at Wenlock Edge but no details of localities were given. Furthermore they supposed that masses of algae together with corals and stromatoporoids were engaged in the building of the Ballstones (Hill 1936, Butler and Oakley 1936, Whittard 1952). Likewise the Crog Balls (found at Dudley) were believed by these authors to be the result of algal decomposition. As far as is known there have been no published records of calcareous algae obtained from the Bringewood Beds (Aymestry Limestone) of this area.

Only a very few of the published accounts mention the genus *Girvanella*. *G. problematica* recorded by Wethered (1890, 1893) was asserted by Garwood (1931) to be 'Sphaerocodium' munthei which is now recognized as an association of *Rotlipletzella* and *Wetheredella* (Wood 1948). *G. conferta* (Chapman) appears to belong to the genus *Rotlipletzella* as it possesses dichotomous branching. The only other record was by Crosfield and Johnston (1941) who noted the presence of algal fragments in the Crog Balls of the Wren's Nest, Dudley, but gave no evidence to show whether they belong to the genus *Girvanella*.

When the present research began, there was little known about Silurian calcareous algae of the Welsh Border and no *Girvanella* records were identified to the species. The

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commonest algal genus, Girvanella, was found to vary so much that it did not appear valid to retain all variants at generic level, or to regard them as related to the Ordovician type, G. problematica. It seems possible that the species of Silurian filamentous algae were numerous and also similar forms could associate together as do living



TEXT-FIG. 1. Reference map of the Welsh Border showing the important areas for *Girvanella*. ca, Craven Arms; du, Dudley; H, Hereford; GM, Great Malvern; LB, Ledbury; LH, Longhope; LU, Ludlow; MF, Mordiford; MW, Much Wenlock; NS, Nash Scar; o, Onibury; OR, Old Radnor; P, Presteign; WH, Woolhope.

forms today. Slight dissimilarities in filament character would not necessarily be reflected in the fossils although several different types of filamentous algae have been proved.

The genus *Girvanella* is subdivided here on filament size and mode of growth which includes branching habit, encrusting and non-encrusting, attached and free forms, the constancy of tube diameter, curvature of tubes, and the amount of adherence between tubes. Several species have similar modes of growth and are grouped together. They can be distinguished by their filament size. A full account of these and other algae can be found in Green (1955, 1959).

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METHODS OF SAMPLING AND EXAMINATION

The presence of Girvanella was rarely found to be indicated by macroscopic structures in the limestones investigated so a suite of specimens from each exposure was examined. Specimens were also taken at intervals along bedding planes. Particular attention was directed to beds in the neighbourhood of reef or reef-like structures where changes in the character of the limestone were likely to be rapid. Thin sections were found to be the most satisfactory for the study of the algae. Measurements on algal material were made by using camera lucida drawings mostly at magnifications of $\times 350$ and $\times 600$. The accuracy of this method was checked by measurements from photographs and also by direct measurements using an eyepiece micrometer scale.

The method used to determine the diameter of algal filaments was to measure the internal diameters of five tubes per specimen to give the range of variation and probable mean. With indistinct groups, the variation is greater, due to increased error in measurement. Longitudinal sections of the tubes were found to be more satisfactory in giving the true diameter. These were compared with tubes seen in cross-section as in the method used by Wood (1957, 1963), but Wood's method was found to be less accurate when measuring finer filaments of 5 μ or less in diameter. Furthermore it was difficult to distinguish transverse and oblique sections especially in fine tubes with thick walls or curving filaments when applying Wood's technique. In many sections the position of the original wall is marked by the greatest concentration of calcite dust (Wood 1941) against the clear calcite of the lumen, and, except in indistinct groups, this darker concentration of dust can be used to determine the original diameter of a filament. This criterion has to be used with caution however, for the calcite dust of the wall may partly obscure the clear lumen in some longitudinal sections.

Crushing of an algal filament is unlikely to occur before death owing to its internal pressure. Flattening only appears to occur when tubes are adherent to each other and nearly always in encrusting forms where the filaments are in a felted mass. Where crushing has occurred, the clarity of the wall disappears and this gives a good indication of the doubtful value of any measurements taken.

The number of each species of *Girvanella* examined by the above method is as follows: 3 specimens of *G. problematica* var. *lumbricalis*, 40 *G. effusa*, 60 *G. ramosa*, 70 *G. fragila*, 85 *G. media*, 95 each *G. sarmenta* and *G. prolixa*, 115 *G. pusilla*, 125 *G. incompta*, and 160 *G. problematica*.

MORPHOLOGY AND SYSTEMATIC POSITION OF THE GENUS

Class POROSTROMATA Pia 1927 ex Harlan Johnson 1959 Genus GIRVANELLA Nicholson and Etheridge 1878

Type species. Girvanella problematica Nicholson and Etheridge.

EXPLANATION OF PLATE 6

Figs. 1, 2. *Girvanella* cf. *prolixa* sp. nov., showing septation and possible heterocyst. MF 1, Woolhope Limestone, GSM. PF 2838/1. 1, ×220. 2, enlarged view ×1000.

Fig. 3. *G. prolixa* sp. nov. with septate filaments. MF 1, Woolhope Limestone, GSM. PF 2837/5; ×220. Fig. 4. *G. sarmenta* sp. nov. Tubes seen in cross-section. WE 11, Wenlock Limestone, GSM. PF 2845/2; ×180.



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Original Diagnosis. 'Nodules composed of microscopic tubuli, with arenaceous or calcareous (?) walls, flexuous or contorted, circular in section, forming loosely compacted masses. The tubes apparently simple cylinders, without perforations in their sides, and destitute of internal partitions of a similar kind.' Wood (1957) in his redescription of the type species of Girvanella does not give a formal emended diagnosis of the genus.

Description. The original diagnosis gave the tube diameters as 10μ and 18μ but later descriptions have considerably extended this range of diameter (Wethered 1889–93, Høeg 1932, Wood 1957, Johnson et al. 1959). During this investigation Silurian members of the genus Girvanella were observed to have a range in diameter from 2 to 31μ . All the filaments examined had the fine granular calcite 'dust' wall (Wood 1941), which was occasionally iron stained, and enclosed a lumen of clear calcite crystals. Aggregations of opaque iron ores including pyrite were found within the lumen in some specimens. The mode of growth was found to be variable. The specimens investigated ranged from parallel sets of filaments having each tube of even diameter throughout to highly contorted filaments with variable diameters; from a loose non-adherent arrangement of tubes to tubes in contact or adherent to each other; from no branching to highly branched forms; and from free living, possibly floating plants to attached forms, encrusting or associating in composite growth with other algal genera. Another feature not recognized in the original diagnosis is one of possible septation (Pl. 6, figs. 1–3).

Definite reproductive organs are unknown within the genus and this may also be the result of indifferent preservation or that the main method of reproduction was by fragmentation of the filaments. A possible 'heterocyst' has been found in one instance with a general rounding of a septate filament which did not appear to be a cut branch as no fracturing of the clear lumen was visible. The 'heterocyst' was oval in shape (Pl. 6, figs. 1, 2) and appeared to be an integral part of the filament rather than a protuberance from it.

From the evidence stated in the foregoing paragraphs it would appear that the formal diagnosis of the genus *Girvanella* requires some revision. Since, however, it is the purpose of this contribution to describe the Silurian species of *Girvanella*, a discussion of the Ordovician type material is not included. The genus *Girvanella* is used in this work in agreement with previous workers though it is suggested that later studies may well lead to subdivision of the genus.

Lower Palaeozoic species and varieties. Høeg (1932), in describing the Ordovician algae from the Trondheim area, subdivided Girvanella problematica into three varieties by differences in size and habit, viz. vars. typicalis, moniliformis, and lumbricalis. In 1942 Lewis reviewed the various Ordovician Girvanella and concluded that they were all varieties of G. problematica including his new variety G. spiralis from the Lévis group, Quebec, and G. ocellata which had been described by Seely (1885) under the genus Strephochetus. Silurian Girvanella have not been similarly subdivided and the present work has shown that they have a different range of form from their Ordovician counterparts. Girvanella from the Welsh Borderland was found to be divisible into eight distinct growth types as follows:

1. Sets of parallel or sub-parallel filaments of apparently unlimited growth, at least

partly adhering to each other as in the G. problematica var. moniliformis Høeg (1932) or as faggot-like bundles.

2. A loose coiling of filaments as in *G. problematica* (redefined by Wood 1957), or more specifically in a coil (as in *G. problematica* var. *typicalis* Høeg 1932). Branching here is infrequent, absent, or in limited portions only.

3. Short curved loose filaments, sparsely branched, sometimes encrusting, correspond-

ing in form to G. problematica var. lumbricalis (Høeg).

4. A spiral development of a single filament (or a few filaments) as in var. *spiralis* (Lewis).

5. Tight coiling of the filaments within a group. This is usually the result of adhering, much branching, curving filaments.

6. Highly branched, curved filaments with uneven diameter, not strictly in a coil but

matted together.

- 7. A 'raft'-like development, probably a variety of the parallel tubes growth form (1) but where the filaments are of approximately equal length and appear to be of limited growth. Tubes are adherent.
- 8. Encrusting forms which may be one or more of the above growth forms.

The tube diameter of these growth forms were also compared and from this data subdivision into district species was found to be possible. Four species groups have been erected for the Silurian *Girvanella*.

Group A SARMENTA (growth form 1 and rarely 7)

Description. Groups of parallel filaments mostly adherent to each other. In longitudinal section appearing as long tubes (tubes of indefinite length), mainly in contact, unbranched or with scarcely any branching. In transverse view the circular cross-sections are arranged in clusters.

Remarks. Normally, no indications of any attachment to substratum are visible. Only in a few specimens do the tubes appear to arise from one end. Raft-like forms are at present included as smaller specimens of this group. Division into species within the group is on the internal diameter of the tube, which varies from 2 to 31 μ .

Species. Girvanella sarmenta sp. nov., G. prolixa sp. nov., G. fragila sp. nov.

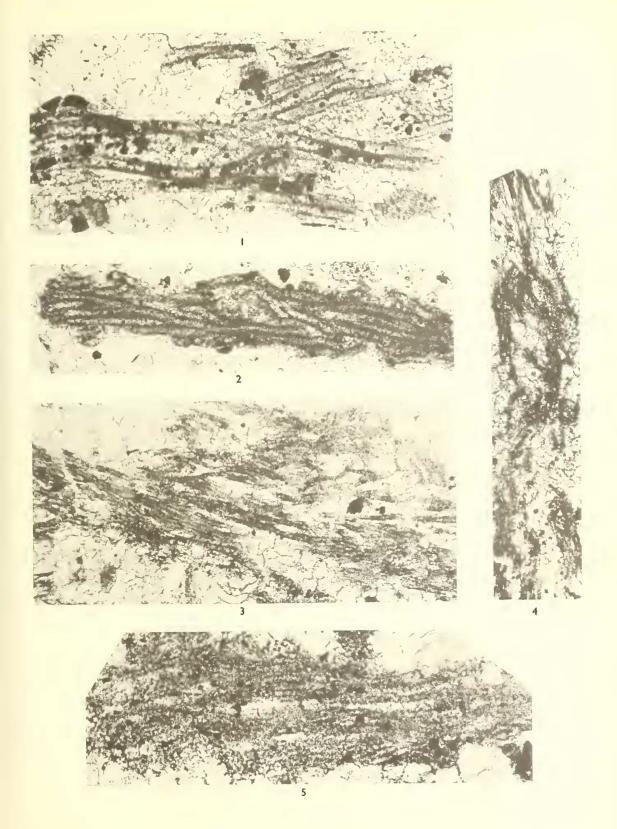
Group B PROBLEMATICA (growth forms 2, 3, 4, sometimes 8)

Description. Loosely coiling or tangled groups. Tubes mostly not in contact with each other. Branching infrequent or none. Tubes do not lie parallel or if they attain a subparallel direction they are mostly not adherent to each other.

EXPLANATION OF PLATE 7

Figs. 1, 2. *Girvanella sarmenta* sp. nov. 1, Holotype; only part of specimen figured. Length of specimen 2·6 mm. Tubes elongate and of even diameter. WE 15, Wenlock Limestone, GSM. PF 2846/4; × 160. 2, Paratype; WE 15, GSM. PF 2846/3; × 140.

Figs. 3-5. G. fragila sp. nov.; MF 1, Woolhope Limestone. 3, 4, Holotype; different sections of the same specimen (figs. not in alignment); GSM. PF 2839/1. Length of specimen 2.5 mm.; ×140. 5, Paratype; specimen with slightly larger tubes, GSM. PF 2837/1; ×180.



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Remarks. Internal diameter of tubes ranges between 2 and 28μ . Branching occurs more frequently in the larger forms. Also in the larger forms, the tubes tend to be more adherent to each other than in the finer-tubed specimens. A variation of this is a tight coiling of filaments of even diameter over each other. The extreme variety of this is the production of a spiral form usually by one filament.

Species. G. problematica, G. pusilla sp. nov., G. incompta sp. nov. (probably including G. problematica var. spiralis Lewis). G. problematica var. lumbricalis may represent a distinct species (growth form 3).

Group C MEDIA (growth form 5, sometimes 8)

Description. Groups of filaments tightly coiling and adhering branching clusters. Branching fairly frequent. Tubes even diameter throughout with apparently no constrictions. Internal diameter $8-18 \mu$.

Species. G. media sp. nov.

Group D RAMOSA (growth form 6, sometimes 8)

Description. Forms characterized by highly branched adherent tubes usually in clusters. Branching irregular. Tubes uneven in diameter and length between branches short.

Remarks. Constrictions are often visible. Groups are sometimes encrusting. The internal diameter range is usually between 11 and 27 μ , rarely more. The group is distinguished from G. media by its irregular diameter and more frequent branching and by its irregular type of branching from the dichotomous branching of a Rothpletzella.

Species. G. ramosa sp. nov., G. effusa sp. nov.

SPECIES DESCRIPTIONS

Group SARMENTA

Girvanella sarmenta sp. nov.

Plate 6, fig. 4; Plate 7, figs. 1, 2; text-fig. 3g

Diagnosis. A non-encrusting Girvanella with bundles of parallel, even diameter tubes with no constrictions. Tubes seldom branch and are mostly adherent to each other. Filament, or internal tube diameter $18-31 \mu$, the majority having diameter between 19 and 22μ .

Holotype. GSM. PF 2846/4; Plate 7, fig. 1. Wenlock Limestone, Silurian. Wenlock Edge, WE 15(5), SO 856455.

Paratype. GSM. PF 2846/3; Plate 7, fig. 2. Same locality and horizon.

Description. This species is one of the largest Girvanella found in these Silurian limestones. Within the Sarmenta group, the narrowest diameter tubes of this species just overlap the range for G. prolixa, but the mean value for the filaments is 5μ greater. It also appears to correspond to the Ordovician G. problematica var. moniliformis (Høeg) in size and longitudinal view but differs from it in transverse section in having tubes arranged in clusters and not in a single row.

There does not appear to be any marked tapering to one end of a cluster so there is no evidence of this form being attached to a substrate.

Distribution. Woolhope and Wenlock Limestones of the Woolhope Inlier and Wenlock Edge. It is infrequent in the Woolhope Limestone. Most specimens have been found at the south-west end of Wenlock Edge although it has been found at the other localities in the Wenlock Limestone on the Edge and at Fownhope.

Girvanella prolixa sp. nov.

Plate 6, fig. 3; Plate 8, figs. 2-4; text-fig. 3d

Diagnosis. Girvanella occurring in small groups of parallel tubes, mostly adhering, sometimes free. Filaments long, with circular cross-section, even diameter and nearly straight. Range of filament diameter $12-18 \mu$, occasionally more. Most filaments are between 14 and 16μ wide.

Holotype. GSM. PF 2840/2; Plate 8, fig. 2. Grey Measures, Wenlock Limestone. Silurian. Farley Quarry, north of Much Wenlock, Wenlock Edge, Shropshire WE 3(7), SJO 15629.

Remarks. Specimens examined from the Wenlock Limestone at Fownhope were found to have tube diameters mostly between 17 and 18 μ wide, which is slightly larger than average. The Fownhope district appears to have been favourable for calcareous algae so it is possible that some algal growths may have been better developed than elsewhere. Some specimens from Fownhope show possible septation in the tubes (Pl. 6, figs. 1–3).

In a very few cases, the filaments partly converge at one end, which could indicate that some of these plants may have been attached during life. Another indication of this may be the 'rafts', shorter length groups which may have formed either part of a larger group or an early stage. In some, the adherent tubes converge to a narrow region and end either by the tubes joining or overlapping.

Distribution. The Woolhope and Wenlock Limestones of the Woolhope Inlier and the Wenlock Limestone of Wenlock Edge. It is occasional in the Woolhope Limestone at Mordiford, but is more common in the Wenlock Limestone. It is abundant in the Grey Measures of Wenlock Edge near Much Wenlock and to the north-east although it has been obtained from most of the exposures examined along the Edge.

Girvanella fragila sp. nov.

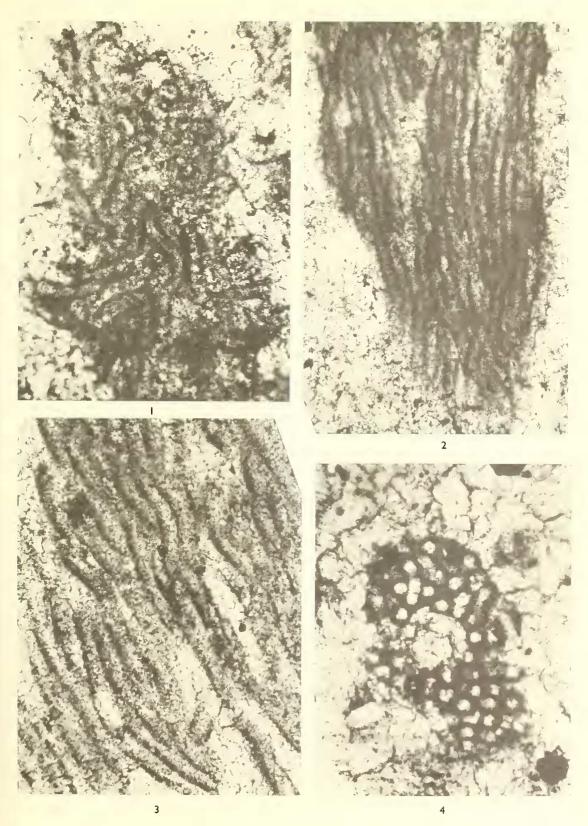
Plate 7, figs. 3-5; text-fig. 3a

Diagnosis. Girvanella in which the tubes are parallel, of even diameter in bundles, mostly adherent, occasionally partly free. Tubes long, straight or slightly undulating. Branching

EXPLANATION OF PLATE 8

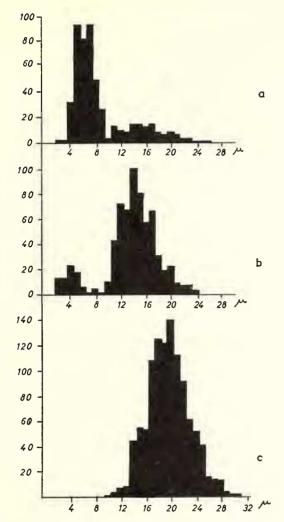
Fig. 1. Girvanella media sp. nov. Small cluster branching tubes mostly adjoining tubes in contact. FH 2, Wenlock Limestone, GSM. PF 2841/3; × 250.

Figs. 2–4. *G. prolixa* sp. nov. 2, Holotype showing sub-parallel tubes, slight branching; WE 3, Wenlock Limestone, GSM. PF 2843/1; × 200. 3, Specimen with sub-parallel tubes slightly larger than average; FH 2, Wenlock Limestone, GSM. PF 2840/2; × 250. 4, Transverse section of tubes; MF 1, Woolhope Limestone, GSM. PF 2837/6; × 260.



JOHNSON, Silurian Girvanella





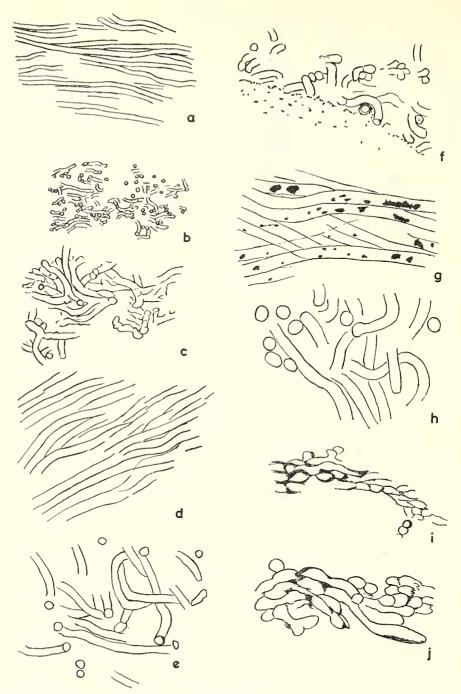
TEXT-FIG. 2. Range of diameter of *Girvanella* tubes from Mordiford, Fownhope, and Wenlock Edge. Five measurements were taken from each *Girvanella* specimen, thus giving the variation for each group and also more overlap of sizes than if the mean only is used. a, Mordiford, 148 specimens measured; b, Fownhope and c, Wenlock Edge, 162 and 164 specimens respectively.

rare. Internal diameter of tubes range from 2 to 9 μ , mostly 5–7 μ , very occasionally to 10 and 11 μ .

Holotype. GSM. PF 2839/1; Plate 7, figs. 3, 4. Woolhope Limestone, Silurian small exposure at junction Littlehope Lane and Mordiford Road, Haugh Wood, Mordiford MF 1(2), SO 373578.

Paratype. GSM. PF 2837/1; Plate 2, fig. 5; same locality and horizon.

Description. The mean value of filament diameters (or the internal diameters of tubes) was found to be 6μ for the Woolhope specimens but the only Wenlock Limestone



TEXT-FIG. 3. Comparative drawings of Silurian Girvanella all at magnification \times 125, showing the size and growth forms of the different species. (Opaque inclusions also indicated in g; tube diameter slightly above average in d and i.)

a, G. fragila sp. nov. b, G. pusilla sp. nov. c, G. media sp. nov. d, G. prolixa sp. nov. from Fownhope. e, G. problematica Nich. and Eth. f, G. problematica var. lumbricalis Høeg. g, G. sarmenta sp. nov. h, G. incompta sp. nov. i, G. ramosa sp. nov. j, G. effusa sp. nov.

specimen had a tube range of $2-4 \mu$. The tubes mainly have very dark grey granular calcite walls, 'algal dust' (Wood 1941). Branching may occasionally occur but is not readily visible.

Remarks. No processes of attachment were seen and as these forms were abundant in bedded limestones away from reef structures, it is possible that this species may have been a floating form. G. fragila and G. pusilla constitute the finest tubed Silurian species found. G. fragila can be distinguished readily from G. pusilla by its different growth habit, the latter being loosely coiled.

Distribution. This species has been found in the Woolhope Limestone around Mordiford where it is abundant at various horizons from just above the Petalocrinus Limestone to nearly the top of the Woolhope Limestone. It is extremely plentiful in the Scutterdine Quarries (Pocock 1930), sometimes appearing to be the dominant fossil in thin section. In the Wenlock Limestone the only specimen was found at Fownhope. No specimens were found in the limestones above this horizon.

Group PROBLEMATICA

Girvanella problematica Nicholson and Etheridge 1878

Plate 9, fig. 1; text-fig. 3e

Neotype. Figured by Wood (1957), Plate 5, fig. 2. Slide BM(NH) V34566. Stinchar Limestone, Ordovician, Tormitchell, Girvan, Ayrshire.

Description. Loosely coiling filament clusters with internal tube diameters 12–18 μ , occasionally more but mostly 15–16 μ , from the Silurian have been included in this species. This corresponds with Wood's redescription of the type species having average external tube diameters 21–22 μ ranging from 18 to 25 μ (rarely 30 μ) and internal diameter average 15–16 μ ranging from 13 to 20 μ (rarely 22 μ). Girvanella having adherent or tight branching or faggot-like groups are not here included. G. problematica has been found both as loose non-encrusting coils and encrusting brachiopods, crinoid ossicles, bryozoa, and tabulate corals.

Distribution. Woolhope, Wenlock Limestones, and the Bringewood Beds. This species is fairly common in the bedded Woolhope Limestone at Mordiford and a few specimens have been obtained from Old Radnor and Woolhope. It is fairly common to abundant in the Wenlock Limestone of Dudley, Fownhope, and Wenlock Edge, especially near Much Wenlock. It has been found also at May Hill, Ledbury, West Malverns, and Sollers' Hope, and is present in the Bringewood Beds (Aymestry Limestone) of Ledbury, View Edge (Craven Arms), and the Whitcliffe Beds, Ludlow.

Girvanella problematica var. lumbricalis Høeg

Plate 9, fig. 2; text-fig. 3f

1932 Girvanella problematica var. lumbricalis Høeg, pl. 1, fig. 6.

Description. Short strongly curving tubes, sometimes encrusting, but if so, only a small area of tube is in contact with the substrate (Pl. 9, fig. 2). Tubes non-adherent,